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SECONDARY-SIGNAL CONTROL IMPULSES, ELECTRICAL
REACTIONS AND SENSITIVITY OF ANALYZERS.

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CHAPTER VI: SECONDARY-SIGNAL CONTROL IMPULSES, ELECTRICAL REACTIONS AND SENSITIVITY OF ANALYZERS.

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ABSTRACT: Many investigators have shown conclusively that the amplitude and latent period of evoked potentials (in direct stimulation in man) are dependent on secondary-signal effects produced by verbal instructions used in the experiment. In addition to the evoked potentials, other aspects of the electrical activity of the human brain may undergo significant changes under the influence of verbal stimuli (depression of alpha rhythm, etc). Many recent works indicate that the sensitivity of analyzer systems is a much more complex function than was heretofore believed. There may be a difference in the excitability of various links in the ascending afferent pathway, and regulatory mechanisms may alter the functional states of all the structures in the analyzer.

In our experimental investigations, which make up the contents /217 of the preceding chapters of this monograph, the effects of the secondary-signal control impulses (expressed in terms of local changes in the excitability of analyzers) were estimated in terms of the latent period of the motor reactions tested. In the preceding sections, however, our conclusions were drawn on the assumption that it is possible to get an idea of the excitability of neuron structures by observing several different indicators. These include (in addition to the latent periods of reactions) the threshold force of the stimuli and the magnitude of the response reaction. Likewise, it is clear that we can use as an indicator of the excitability of certain nervous structures, parameters which are not merely motor reactions but may be any other reactions, under the condition that the nervous excitation in these reactions takes place by means of structures which are interesting to the investigator.

Assuming this point of view in evaluating several items in the literature dealing with the investigation of analyzer systems in man, we came to the conclusion that a great many of the experimental factors involved here, which depend on the effect of verbal stimuli on the operating parameters of the analyzer, can be satisfactorily understood in terms of theories which have been developed regarding secondary-signal control impulses.

* Numbers in the margin indicate pagination in the foreign text.

In the present chapter, we shall adopt this point of view in considering the effect of verbal stimuli on electrical reactions and the sensitivity of analyzers in man. In this way, we will attempt to show that the data obtained when using other criteria for excitability are completely in agreement with the results which we obtained from an analysis of the latent period of the test reaction. In addition, it will become clear in the course of the discussion that the use of various methods and indicators of excitability in a number of cases makes it possible to widen and deepen our understanding about the functions of secondary-signal control impulses.

§1. Secondary-Signal Control Impulses and Evoked Potentials (EP).

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In a number of investigations, it has been shown conclusively that the amplitude and the latent period of the evoked potential¹ (in the case of direct stimulation in man) are essentially dependent on the secondary-signal effects caused by the verbal instruction used in the experiment. Garcia-Austt, Bogacz and Vanzulli (1964) recorded EP's from the occipital region of adult subjects in response to rhythmic light flashes with a frequency of one per second and one every two seconds. The experiments were conducted under neutral conditions (the subjects were not given instructions of any kind except for instructions on where to look) and under the condition that the experimenter told them to count the light flashes, to indicate any changes in their intensity or frequency, or to direct their attention to the presence of after-images. In analyzing the EP's (which as a rule showed up with insufficient clarity when recorded from the surface of the skull), the method of averaging was used. 20 to 40 responses to successive light pulses were averaged.

The investigation showed that instructions of all three types regularly led to a noticeable increase in the EP amplitude; the shape of the EP's was frequently complicated as well: under these conditions, it most often showed several successive oscillations. The authors also noted the following interesting facts: In several cases, when the subjects made statements about the presence of rapidly appearing positive after-images in response to one flash, two full-valued potentials were recorded with an interval of 80 to 100 msec. between them. How can we interpret the facts observed?

The increase in the amplitudes and the decrease in the latent period of the EP's, in the opinion of a number of investigators, are the consequence of an increase in the synchronism of the neuron discharges which generate EP's (Narikashvili, 1963, Gershuni, 1965).

¹ By evoked potentials, we mean the primary and secondary responses, which cannot be differentiated (especially in the majority of the investigations discussed below) and are referred to by the general term "evoked potentials".

But the increase in the synchronism of the neuron discharges may in turn be caused by different factors: an increase in the afferent signals arriving, an increase in the fixed rise time for the signal as well as equalization and an increase in the level of excitability of the entire combination of neurons which take part in generating the EP's (Narikashvili, 1963).

If we analyze the experimental conditions described by Garcia-Austt, Bogacz and Vanzulli, we must conclude that the first two possibilities of changes in the characteristics of the EP's are completely inapplicable here. It is true that there were no additional changes in the characteristics of the visual stimuli in the experiment. The only respect in which the various experimental situations differed from one another consisted in the presence or absence of advance instructions, intended to cause certain mental operations when the signals were displayed. Consequently, only the verbal sections of the cortex and the control impulses associated with them can be considered responsible for the increase of the EP amplitudes in the situations in question. But if this is the case, then this is the entire basis for combining the results of the experiment analyzed above (and all other similar experiments which will be considered later on) with data given in the preceding chapters regarding the mechanisms of the regulatory function of the second signal system in the higher nervous activity of man. /219

These data showed that the verbal sections of the cortex control the processes of analysis and synthesis of direct stimuli by means of changes in the excitability of the analyzers of the primary signal system. Therefore, we may assume that these same changes in excitability (an increase in its level) evoked by preliminary verbal instructions are also expressed as changes in the EP characteristics in the projection sections of the cortex. In addition, there is also a basis for assuming that in this case we are talking about a previously prepared increase in the excitability of the visual structures which precedes each flash, and not about the special effect of secondary-signal control impulses. This conclusion is based on the following:

The latent periods of the EP's recorded and analyzed in this and similar experiments are short. As a rule, they do not exceed 50 msec. and are consequently much shorter than the critical time, when it is possible to observe a special activity of the secondary-signal control impulses with respect to visual projection. (According to the data of a number of investigators presented in chapters 3 and 5 of this monograph, this time is at least 200 msec. from the beginning of the stimulator activity, which causes activation of the secondary-signal control impulses). Hence, we must assume that in the case under consideration the increase of the EP amplitudes takes place because, under the influence of the verbal instructions, the visual stimuli reach regions of the cortex whose excitability has already been elevated by means of secondary-signal control impulses of a tonic nature. Consequently, in the given case (as in the ex-

periments analyzed in chapter 3 of this monograph) the increase in the excitability of the visual analyzer is the necessary condition which insures carrying out of the preliminary instructions.

The abovementioned ideas also apply to all other experiments with EP recording in man which will be discussed below, inasmuch as all of them were conducted in essentially similar conditions. Hence, we will not draw any conclusions in what follows regarding the problems posed here. However, before proceeding to a discussion of the other material dealing with the effects of instructions on EP's in man, we should turn our attention to still another fact. All of the investigations which we are discussing in the present chapter were conducted under conditions of monopolar EP recording. From the methodological standpoint, this is more accurate than bipolar recording (Meshcherskiy, 1965). /220

The significance of the functional shifts in excitability, which are related in human analyzers to secondary-signal control impulses in the presence of analytic-synthetic activity, have already been discussed in detail in chapter 3 of this monograph. Similar conclusions follow from the results of extremely interesting and conclusive investigations by Haider, Spong and Lindsley, in which the magnitudes and latent periods of EP's produced in response to light pulses served as the measure of cortical excitability (Haider, Spong and Lindsley, 1964). The authors recorded EP's in response to light pulses at the visual cortex, recording from the surface under conditions of specific problems of long-term attention and observation (vigilance tasks). The experimenter required the subjects to make rather sharp differentiations between the visual signals given. For a period of 80-100 minutes, the subjects looked continuously at periodic light flashes on a screen located in front of them. The screen was illuminated once every three seconds, but there were no advance warnings of any kind. The screen was illuminated first by a bright light (15 lamberts) then by a dim light (9 lamberts). The dimmer flashes were given much more rarely than the bright ones and the subjects were required (according to the instructions) to indicate when they had seen a dim flash by pressing on a telegraph key. In this experiment, along with the EP's the experimenters recorded the number of correct reactions and all the dim flashes which were missed. The EP's in response to the bright flashes were averaged for equal periods of time (5 minutes). The EP's in response to the dim flashes were averaged over the entire experiment, separately for those flashes observed by the subject and for those that were missed. The following results were obtained:

(1) The amplitude of the EP's obtained in response to the bright flashes gradually decreased from the beginning to the end of the experiment and the latent periods of the EP's gradually increased. These changes in the EP's were accompanied by a decrease in the number of dim flashes observed; this behavior did not change during the experiment.

(2) The amplitude of the EP's in response to the dim flashes observed was much greater than the amplitude of the EP's in response to the same dim flashes when missed by the subject.

The data of Haider, Spong and Lindsley are very significant. They make it possible to conclude, with a high degree of certainty, that the changes in the excitability of the visual structures of the brain (expressed as changes in the EP's in response to light stimuli) cause changes in the behavioral reactions which are governed by these central structures. We must conclude that the fine differentiation of visual stimuli (under the conditions of the problem of a vigilance task) requires a rather high level of excitability of the visual analyzer. Hence, the increase in excitability here becomes the necessary condition for reaching the set goal and must be combined with (and reinforced by) the secondary-signal control impulses. Any weakening of these impulses or weakening of their effects in the analyzer means that the goal which is set for the subject fails to be fulfilled in the required manner: he misses the light flashes. /221

A very characteristic feature is a change in the EP in response to direct stimulation under experimental conditions, with reaction to preliminary verbal instructions. Thus, Larsson showed that if preliminary instructions are required for the subject to react as rapidly as possible by a motor reaction to a given stimulus, then the EP in response to the stimulus increases considerably, both in projection regions which are specific for the given stimulus and in other areas of the cortex (Larsson, 1959).

An increase in the amplitude of the EP's in the auditory region with surface recording during accomplishment of differentiation reactions was noted by Davis (1964). In his experiments, Davis recorded EP's in response to four successive tones. Three series of experiments were performed. In the first series, the subjects read newspapers while the tones were being produced. In the second series, they would press a button after hearing the third tone; in the third series, they pressed the button after the third tone was produced only if it was louder than the second. In the latter case, a significant increase in the EP amplitude was observed. Recalling all the previous data and keeping in mind the very short latent period of the EP's, we can say that these data agree completely with the data presented in Chapter 5 of this monograph. The changes in the EP as well as the latent periods of the test reactions also indicate the existence of an increased excitability of the projection areas of the brain which (in the experiment with the reactions) precedes the action of the triggering stimuli.

The influence of the previously prepared increase in the excitability of the nervous structure on EP's also shows up clearly in the investigation of I.A. Peymer (1958). I.A. Peymer recorded EP's in response to light in the visual and motor regions of the cortex so that (as in the previous investigations) he could average

the individual responses. When the light pulses, according to the instructions, were made signals for motor reactions, a significant change in the EP's was observed. Their negative phase increased in the occipital region, while there was an increase in EP amplitude in the motor region. In addition, the motor region showed a significant shortening of the latent period of the EP's. These facts are also in good agreement with the conclusions drawn in the preceding chapter relative to the mechanism of the production of motor reactions with preliminary instructions, under the conditions of absence of differentiation or with a small number of differentiation stimuli. /222

The shortening of the latent periods of the EP's in response to light in the experiments of I.A. Peymer (not only in the visual but also in the motor regions of the cortex) and the increase in the amplitudes of these EP's once again indicates that in the absence of any reaction the previously prepared increase in excitability takes place not only in the sensor structures but in the motor structures as well.

From the point of view of an analysis of the mechanism of the carrying out of reactions, it is especially interesting to consider the investigation of I.A. Peymer and M.L. Modin (1963), which was specifically concerned with comparing the latent period of the EP's produced by triggering visual stimuli in the absence of a simple motor reaction on the one hand, and differentiating reactions on the other. The authors found that with the transition from a simple reaction to the differentiation of two stimuli, the latent periods of the EP's lengthened while the amplitudes of their negative phases decreased. We may assume that these data are a direct indication of a greater increase in the excitability of the sensory areas of the brain under conditions of a simple reaction than under conditions of differentiating reactions. Hence, they can be used as still another argument in favor of theories dealing with the reduction of the degree of preliminary increase in excitability of nervous pathways upon transition from a simple motor reaction to an essentially differentiating reaction. Such theories were discussed in the preceding chapter of this monograph.

The results which were obtained in the work of I.A. Peymer and M.L. Modin are apparently still more convincing in the light of data obtained in the investigations of Donchin and Lindsley (1966). The investigations of these authors conclusively demonstrate the causal relationship which exists between the excitability of the afferent structures of the brain (expressed by the values of the EP amplitudes) and the speed of the motor reactions, evoked by the corresponding trigger signals. In their experiments, Donchin and Lindsley recorded the latent periods of simple motor reactions to visual stimuli and the EP's which arose in response to these stimuli in the occipital region of the cortex and in the vertex region. It was found that the higher amplitude EP's always corresponded to more rapid reactions and *vice versa*.

This conclusion was based on an analysis of experimental data /223 of two kinds. First of all, it was found that the amplitudes of the EP's in response to visual stimuli were higher when the subjects were stimulated to reactions of maximum rapidity by means of preliminary instructions and stimulating actions on the part of the experimenter. Secondly, averaging the EP's separately for all the reactions with short latent periods (below the median) and all the reactions with a prolonged latent period (above the median) showed that the EP amplitude was significantly higher in the first case than in the second. Generalizing all of these data, the authors reached a conclusion with which we completely agree and consider to be of the greatest interest: The changes in the amplitudes reflect changes in cortical excitability, while the latter are the direct cause of changes in the latent periods of the reactions.

Changes in the EP's in response to sensory stimuli, under the influence of a different type of verbal stimulation, were observed in a number of investigations which are of interest in this regard, thanks to the peculiarities of the recording of the electrical responses. We have in mind papers by Hernández-Peón and Donoso (1959), Jouvét and Courjon (1959), Jouvét, Lapras and Hermann (1959), as well as Jouvét et al. (Jouvét, Schott, Courjon and Allégre, 1959).

In these investigations, the EP recordings were not made from the surface of the skull, but rather by means of electrodes located in separate subcortical structures of the brain (optic chiasm and geniculate nuclei of the thalamus). The results obtained in these papers revealed several new properties of secondary-signal changes in excitability which could not be explained by using any other methods of investigation. The data obtained indicate that the changes in excitability produced by secondary-signal control impulses are not limited by the cortical regions of the analyzer but included (at least in the case of the previously prepared shifts in excitability) their underlying structures.

Hernández-Peón and Donoso, as well as Jouvét et al., recorded EP's in response to light flashes directly in the region of visual radiation. Consequently, the changes in the EP's in these cases reflected changes in excitability related to verbal stimulation at least on the level of the neurons of the lateral geniculate body. Finally, we cannot exclude the possibility that corresponding changes in excitability propagate still farther toward the periphery of the visual analyzer. At the present time, however, we do not have available any kind of data for drawing any conclusions with regard to this problem

The effect of various verbal instructions upon EP's produced /224 by light in visual radiation turned out to be completely analogous to the effect on the EP in the cortical regions of the visual analyzer. The EP amplitude increased with instruction to count the light flashes. It was also shown that when presenting light flashes of uniform intensity, the verbal suggestion that a strong flash would

follow increased the EP amplitude, while the verbal suggestion that a weak pulse would follow reduced the EP amplitude.

Jouvet, Lapras and Hermann recorded EP's in the somatic nucleus of the thalamus in response to rhythmic stimulation of the skin (pinches of constant force). As in the preceding experiment, instruction to count the pinches or simply to concentrate one's attention on the pinches produced a clear and definite increase in the EP amplitude.

It should be mentioned that in all the investigations discussed in this paragraph, it was also observed that a different kind of distracting stimulus (solution of arithmetic problems in one's head, extraneous stimuli, and so on) lead to a noticeable reduction of the EP amplitude. Reduction of the amplitude was also noted in connection with the influence of extraneous stimuli of the same type (flashes from another light stimulator, bright images of past hallucinations). This latter fact, observed in the investigations by Hernández-Peón and Donoso, deserves special attention. It shows that the stimulation of additional and "extraneous" configurations of neurons in the same analyzer system has the same kind of braking effect on the state of excitability of the configurations in question (which is expressed as a reduction of the EP amplitudes in response to corresponding stimuli), as in the stimulation of other analyzers and other brain structures.

A similar fact in surface recording of EP's in response to light flashes was found in the investigations of Van Hof et al. (Van Hof, Van Hof - Van Duin, Van der Mark and Rietveld, 1962). When the outline of a human figure was flashed onto a screen, periodically illuminated to serve as a stimulus to the formation of the EP, the amplitude of the latter decreased significantly. Consequently, increasing the activity of new configurations of visual neurons slowed down the activity of other configurations related to the perception of the general illumination of the screen.

Completing the analysis of the materials related to the change of the EP in man under the influence of verbal stimuli, we should mention the fact that there are several works in which results were obtained which do not agree with or even contradict those found in all the other investigations which we have mentioned.

In the paper by Van Hof et al. (Van Hof, Van Hof - Van Duin, /225 Van der Mark and Rietveld, 1962) EP's were recorded in 15 subjects from the surface of the occipital region in response to light flashes under "passive" conditions and under conditions when the subjects were counting the flashes according to the experimenter's instructions. Definite changes in the EP with transition to counting of the flashes were observed in only one of the 15 subjects; in this particular subject, however, the changes in the EP took place in complete agreement with the results of all the other similar investigations. The instruction to count the flashes led to a consider-

able increase in the amplitude of the first negative phase of the EP and to considerable shortening of the latent period of their appearance on the cortex. Hence, the results of this investigation are apparently not contrary to or inconsistent with the data of other authors. Instead, they show the presence of a definite and regular increase in EP amplitude in all individuals instructed to count the light flashes which were presented.

As far as actual opposition to the overwhelming majority of facts in this field is concerned, we must mention the data reported by Samson et al. and Callaway et al. (Samson, Samson - Dollifus and Pinchon, 1959; Callaway, Jones and Layne, 1965). According to Samson et al., the EP's in their subjects had maximum amplitude when the attention of the subjects slackened and not when they were stimulated to action by the experimenter. Unfortunately, the authors did not mention precisely how they attracted the attention of the subjects and precisely how much attention was paid to the sensory stimuli and not to some other kind of signal of the same type. The means by which the attention of the subjects is attracted is undoubtedly the most important factor which affects the nature of the change in the EP's. Special attention has been drawn to this by the authors of a number of papers in this field (Van Hof, Van Hof - Van Diun, Van der Mark and Rietveld, 1962; Spong, Haider and Lindsley, 1965).

Translating this idea into physiological language, we would have to say that the nervous processes evoked in the cortex of the hemisphere by a preliminary verbal instruction, which stated that definite actions or operations would have to be carried out when direct stimuli appeared, may be very different in various cases depending on their nature and the degree of excitability. Hence, their influence on the functional characteristics of the cortical cells of direct projection (and frequently on the EP's) may be quite different in different cases. For example, Callaway et al. observed a fall in the EP amplitudes for one of two tones used in the experiments (600 cycles in some cases and 1000 cycles in others) when the subjects (according to the instructions) were supposed to notice small differences in the duration of these tones (Callaway, Jones and Layne, 1965).

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The influence of a different kind of instruction, attracting the attention of the subjects to the stimuli in different ways, was the subject of special investigation in the studies of Spong, Haider and Lindsley (1965). In these experiments, the authors recorded EP's in response to light flashes and clicks presented successively at intervals of 1 second to 13 healthy adult subjects under the following conditions: Three different instructions were given:

(1) Instruction to count stimuli of only one type (visual or auditory). For purposes of control, the subjects were asked to press a button each time they counted 50 stimuli of the same type.

(2) Instruction to press a key when each stimulus of a certain type appeared (upon hearing sounds in some cases and seeing flashes in others).

(3) Instruction to carry out prolonged observation for stimuli of a certain type (vigilance tasks). Under these conditions, the auditory or visual stimuli differed in intensity and the subject had to watch for visual or auditory signals of only one particular intensity and indicate their response by pressing on a key.

The EP's in response to each of the above-described signals were averaged for each experimental series over five-minute periods separately for the visual and auditory cortices. The authors analyzed the average responses to 300 flashes and 300 clicks.

The results of the investigation showed that under the conditions of the second and third type of instruction the EP's were much higher in amplitude for a given type of response which the subject made according to the instructions of the experimenter. The differences in EP amplitude were particularly large under the conditions of the third instruction, which required prolonged observation for stimuli of a particular type. As far as the effects of the first instruction on the nature of the EP's in the visual and auditory cortex are concerned, they were found to be contradictory and varied in different subjects. In six subjects the changes in the EP's had a conventional character, i.e., their amplitude was large for those stimuli which the subject considered to be in accordance with the instruction. In three subjects, under these conditions, no differences at all were noted in the nature of the EP's in response to auditory and visual signals; in the remaining four subjects, the reverse picture for EP changes was found. In the latter subjects, the EP's for those stimuli which required counting (visual or auditory) were less in amplitude than the EP's in response to the signals of the other type.

The investigation of Spong, Haider and Lindsley thus clearly showed that many problems which concern the influence of verbal instructions on EP's in man require further investigation. The problems which arise here are apparently of a dual nature: On the one hand, there are general electrophysiological and neurophysiological problems involving the nature of the EP and the cause of changes in its various characteristics. On the other hand, there are undoubtedly special problems of higher nervous activity in man, related to this special character of the verbal signals and to the different means by which the preliminary verbal instructions are received by the brain. /227

Having considered the influence of instructions on EP characteristics in man, we must now turn our attention to one work which is interesting in the sense that the EP's were recorded in response stimuli which were more complex than usual. This consisted of displaying numbers and letter (Chapman, 1965) which were projected in

series of four on a screen placed before the subjects. Each of the three series consisted of two letters and two numbers, arranged alternately. According to the preliminary instructions, the letters and numbers were used alternately as relevant stimuli. This was achieved as follows: in some cases, the subjects were asked to note which of the two numbers in the series was greater in absolute value. In the other cases the subjects had to state which of two letters came first in the alphabet. Comparison of the EP's for the same numbers and letters showed that their amplitudes were much greater when the corresponding stimuli became the objects of analytical activity as determined by the verbal instructions.

In all of the investigations discussed thus far, stimuli for which EP's were recorded as a response always served as direct film stimuli for one or another motor or verbal reaction. A completely different character is found in the extremely interesting investigation of EP's in man, carried out recently by G. Walter (Walter, 1965; Black and Walter, 1965).

EP's in response to stimuli of different types were recorded by Walter in the anterior lobes of the human cortex, either under neutral conditions or under conditions where there were definite reactions in accordance with preliminary verbal instructions. In the latter case, under the condition that instruction was given to perform a given motion as rapidly as possible (to squeeze a bulb) in response to a certain signal, EP's were recorded not only in response to this trigger signal, but also in response to the warning stimulus which preceded it and was linked to it by the instructions. As the preliminary and performance signals, the experimenters used visual (flashes) and auditory (clicks) stimuli given at intervals of 1 second (in some cases the warning stimuli were flashes and the performance stimuli were clicks; in other cases the order was reversed).

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Walter was able to show very clearly and unambiguously that instruction to react to the second of the associated stimuli causes a very noticeable change in the electrical responses to these stimuli in non-specific regions of the cortex. Under these conditions, a prolonged high-amplitude slow negative potential appears between the first and second stimuli. This is the so-called "wave of expectation", or ϵ -wave. This is a negative wave which increases up to the moment when the triggering signal is given, and considerably alters and reduces the EP which arises in response to it. It now appears essentially in the form of a sharp drop in the potential difference to a base line. In addition, if the visual and auditory stimuli are presented within a given interval, one after the other, but the instructions to carry out the motion in response to the second stimulus are absent, both electrical responses will be reproduced with only slight changes. If the notice of a performance signal after the advance signal is dropped (without warning) then the "wave of expectation" gradually decreases in amplitude and finally disappears completely. But warning the subject that the second

stimulus will not apply at all, immediately leads to complete disappearance of the ϵ -wave. Lengthening of the interval by which the secondary signal follows the first caused lengthening of the ϵ -wave, which could be clearly seen for 10 seconds and perhaps more.

A change in the experimental conditions, i.e., some of the warning signals begin to be accompanied by performance signals, leads to a reduction in the amplitude of the ϵ -wave and to production of the conventional EP shape in response to the second stimulus. The amplitude of the "wave of expectation" is then regularly linked with the probability of the appearance of the performance signal and a reaction.

Very generally speaking, these are the principal facts reported by Walter. Although the author himself does not consider the data obtained within the context of a theory of interaction of two signal systems in the higher nervous system of man, we must consider that such a interpretation is entirely logical. This was frequently mentioned by P.K. Anokhin in his discussion of Walter's report at a Moscow symposium on the anniversary of the centennial of the appearance of I.M. Sechenov's work, "Reflexes of the Human Brain". In the opinion of P.K. Anokhin, Walter's experiment has immediate relevance to the problem of a physiological substrate of preliminary verbal instructions. We are completely in agreement with P.K. Anokhin's point of view and will permit ourselves to express some ideas relative to the possible interpretation of the data obtained by Walter, in the light of theories of the mechanisms for regulatory functions of the secondary-signal system in the higher nervous activity of man. /229

From our viewpoint, extreme significance must be attributed to the fact that the latent periods of the evoked motor reaction, as Walter reports, are shortened in the presence of the "wave of expectation" than when it is absent. Hence, the nervous phenomena taking place in the frontal regions of the brain in man after presentation of a warning signal, and finding their electrographic expression in the appearance of a slow high-amplitude negative potential, must be closely related to the shortening of the latent periods of reactions to triggering stimuli. However as we have tried to point out above, a shortening of the latent periods of the motor reactions is related to an increase in excitability of the corresponding nervous pathways. Moreover, on the basis of an analysis of a number of experimental facts, we have also come to the conclusion that this increase in excitability is the result of the action of positive secondary-signal control impulses. According to our theory, these impulses act as direct cortical projections and their source is thought to lie in those regions of the cortex which are related to verbal stimuli. Are there not frontal regions where the phenomenon of the ϵ -wave is recorded, regions which are linked with the source of secondary-signal control impulses for direct projections? If this is in fact the case, then the frontal regions of the brain in man must be viewed as regions which are very closely linked to the presence

of regulatory and control functions of the secondary-signal system.

Unfortunately the scope of the present monograph does not permit us to pause for a discussion of the very complicated and interesting problem about the functions of the frontal lobes of the brain. Let us note merely that at the present time it is generally assumed that in man they have a direct relationship to the existence of complex directed acts, which require prolonged concentration on given goals and evaluation and are linked with the operation of abstract understanding. As far as the connection of the frontal lobes of the brain in man with functions of the speech system is concerned, this is a problem which does not clear to any degree whatsoever.

As we know, I.P. Pavlov, in developing the concept of the secondary-signal system, actually considered the frontal lobes as their substrate, but then changed his point of view. At the present time, only the 44th and 45th fields of this region are usually included among the structures connected with the activities of the secondary-signal system (Sarkisov, 1964). According to the voluminous experimental data obtained by Penfield, a large part of the cortex of the frontal lobe regions does not belong to areas exclusively concerned with speech and is not related to the functioning of the corresponding speech systems in man (Penfield and Roberts, 1964). However, /230 we might assume that the frontal lobes, although not speech areas in the strictest sense of the word, nevertheless are related to the existence of control functions of the secondary-signal system in the higher nervous activity of man. This may be why, as A.R. Luriya reports, massive injuries to these regions lead to an impossibility for patients to submit their will to the verbal instructions of the experimenter, although the entire speech function of these patients shows no signs of disturbance (Luriya, 1963).

The facts reported by Walter, in our opinion, may have enormous significance within the context of the problems under consideration. These facts depend on the significant activity of the neurons of the frontal lobes of the cortex under the conditions involved in carrying out verbal instructions. Therefore, they can apparently be considered as definite evidence that the frontal lobes are actually involved in that complicated process of secondary-signal regulation which begins with the reception of verbal instructions and finishes with an increase in the excitability of the projection segment of the cortex. This leads in turn to a shortening of the latent periods of the motor reactions which are carried out. In this sense, the phenomenon described by Walter may have very great significance for solving problems of higher nervous activity in man and must be subjected to further investigation.

§2. Secondary-Signal Controlled Impulses and Depression of the Alpha Rhythm. Depression of the Roland Rhythm and the Effect of Adopting Rhythms.

Not only the EP's, but other characteristics of the electrical activity of the human brain as well, may undergo significant changes under the influence of verbal stimulation. This fact is also related to the widely known phenomenon of the depression of the alpha and Roland rhythms. It is true that the physiological correlates of the phenomenon of depression are not sufficiently clear at the present time; this makes it difficult to investigate and analyze processes in higher nervous activity. It is well known that blockage of the alpha rhythms occurs when using both positive and inhibitory stimuli. But it has been shown by direct experiments that depression of the cortical activity may correspond either to an increase or a decrease in the excitability of the corresponding structures (Kogan, 1958).

The most definite fact is probably that depression of the basic rhythms of the cortex or a desynchronization reaction are related to the arrival of impulses from the nonspecific subcortical systems of the brain. Here, however, there are other factors which are related to the fact that local desynchronization is not necessarily connected with impulses from nonspecific structures in the subcortex, but may be produced by impulses which propagate along intracortical pathways. However, regardless of the considerable difficulties which arise here, we shall nevertheless present some experimental data which indicate a considerable influence of verbal instruction on the electrophysiological phenomenon under consideration. These facts show that such parameters of depression of cortical rhythms under the influence of direct stimulation, like the latent period and duration, are subjected to the considerable influence of the verbal stimuli of the preliminary instructions. Thus, it was found in a number of papers that the latent period of the blockage of the alpha rhythm, under the influence of light stimuli, is shortened to about 30-40 msec. if the light stimulus (according to the instructions) is a signal for a motor reaction (Travis, Knott and Griffith, 1937; Knott, 1939; Jasper and Cruikshank, 1937). Bakes (1939) also noticed a shortening of the latent period of the blockage of the alpha rhythm as a response to auditory stimuli when they constituted a signal for motor reactions. Several of these authors (Knott, 1939; Bakes, 1938) noted that the latent periods of blockage of alpha rhythm are, as a rule, shorter under the conditions of a simple reaction than under the conditions of differentiation reactions ("choice reactions", to use the terminology of the authors).

From the data which we have examined, we are forced to draw an important methodological conclusion, analogous to the one drawn above in regard to the investigation of conditioned reflexes in man. Inasmuch as the secondary-signal impulses may have a significant influence in changing the characteristics of the electrical reaction

in man, altering (to a certain extent) the latent period of depression, and (as we will show later on) affecting the duration of the depression of the alpha rhythms, all of the secondary-signal conditions of the experiments in investigating the EEG of a healthy adult had to be carefully evaluated and checked. This check was very important, but may be still more important under passive experimental conditions, when no kind of special instructions are given to the subjects regarding the operating stimuli. Thus, Travis, Knott and Griffith described a case where one of the subjects, during an experiment under passive conditions, displayed very short latent periods of blockage of the alpha rhythm in response to light stimuli. As questioning of the subject revealed, this took place when he began to make an effort not to fall asleep. It is natural that the author did not think it possible to use the qualitative data from this subject in comparing the passive and active conditions of the experiment.

The need to take the self-instruction of subjects into account /232 when recording electrical reactions is also important, because the alpha activity itself is evidently (to a certain degree) under the control of secondary-signal effects. Thus, Ford and Yeager (1948) reported that in a state of hypnosis, with the aid of a verbal suggestion to relax, it was possible to obtain a good alpha rhythm in those subjects whose usual EEG showed very low alpha activity. In this respect, we must not omit mentioning that according to the statements of several people, they can will themselves to be in a state that causes a good alpha rhythm to be recorded in the EEG (Simonov, Valuyeva, Yershov, 1964). Although this problem has not yet been investigated, and it is not clear whether or not the influence of the verbal stimuli is direct or indirect, nevertheless this finding must clearly be kept in mind in many instances when analyzing the EEG's of healthy adults.

A comparison of the values for the latent periods of blockage of the alpha rhythm and the latent periods of the motor reactions reveals several points which admittedly may be significant for an analysis of the mechanism of the performance reactions in man. For example, several of the authors cited above noted that in several cases, depression of the alpha rhythm in response to a light signal occurs later than a corresponding motor reaction. This observation may at first glance appear discouraging, but does it not agree with the facts observed (for example) by M.Ya. Rabinovich (1961) in his investigation of the electrical activity accompanying the development and reinforcement of the defensive conditioned reflex in animals? M.Ya. Rabinovich found that as the defensive conditioned reflex is established, the changes in the EEG become more constant and unambiguous in comparison with the period of their production. This conclusion is deserving of particular attention, because recording of the EEG's was carried out in all the layers of the cortex corresponding to the analyzers, thus avoiding the possibility that the author might have "overlooked" some changes in the EEG which occurred regularly.

In addition, M.Ya. Rabinovich found that sometimes, in the case of a reinforced conditioned reflex, no characteristic increase of electrical activity is observed in the analyzer of the positive signal stimulus. However, the electrical activity does decrease. On the basis of these observations, the author comes to the conclusion that in the case of a reinforced conditioned-reflex reaction, the location of the circuit may change during the period of one experimental day and the afferent portion of the reflex arc occasionally shifts to the subcortical links of the analyzer.

Such an interpretation of the facts has raised a number of recent objections (Asratyan, 1965). In the opinion of E.A. Asratyan, the disappearance of pronounced changes in the EEG in response to the repetition of the reinforced conditioned reflex does not reflect a shift of the reflex arc into the subcortex but rather a disappearance of those important functional changes in the cortical structure which take place at earlier stages in the development of the conditioned reflex. /233

Nevertheless, regardless of which of these hypotheses we adopt, we must take into account that the various conditioned reflexes which differ in reinforcement have different electrographic manifestations. Could we not similarly interpret the data obtained in experiments on human subjects? In other words, could not the fact of the unnatural relationship of the latent periods of the electrical and motor reactions be understood as an indication that in these cases the reactions have a different, simpler anatomical structure or occur against a background of smaller functional shifts in the cortical structures?

The probability of such a conclusion is reinforced by the fact that the phenomenon under consideration is more often encountered in simple reactions than in those involving differentiation. According to the data of Knott (1939), the corresponding figures are 10.5% for simple reactions and 2.8% for those involving differentiation. The much higher figures given by Bates (53% for simple reactions and 26% for those involving differentiation) hardly need to be taken into consideration in the given context; in his experiments, while recording the alpha rhythm in the occipital region, he used an auditory stimulus as the triggering impulse. The reaction to the latter was not connected directly with the functional condition of the visual cortex. We shall dwell on this topic in greater detail below.

In this case, we should consider still another work in which special attention was given to the relationship of the latent period of depression of the alpha rhythm to light signals, in the occipital region of the cortex, and in the latent periods of motor reactions with preliminary instructions. Stamm (1952) investigated this relationship in several types of experiments:

(a) Under passive conditions, when the subjects did not re-

ceive instructions to react in any manner to the flashes of light.

(b) Under conditions of a differentiation reaction, when the light served as a positive signal and the sound was an inhibitory differentiation stimulus.

(c) Under conditions of simple reaction, when the subjects reacted with a motor reflex in response to both light and sound.

(d) Under conditions of simple reaction, when only the light flashes were presented at much shorter intervals than usual (about 2.5 seconds apart).

The author found that the latent periods of depression of the alpha rhythm shortened with transition from conditions "a" to conditions "b", but then remained constant. As far as the latent periods of the motor reaction are concerned, they steadily decreased from conditions "a" to "d". Under conditions "d" the latent period of the motor reactions turned out to be much shorter than the latent periods of the blockage of alpha activity. /234

By analyzing the data obtained, the author came to the conclusion that the correlation between the latent periods of the alpha-rhythm depression and the latent periods of the corresponding motor reactions is very small. However, it seems to us that if we analyze these facts, keeping in mind several concrete physiological ideas about the mechanisms of the production of reactions with preliminary instruction, they turn out to be much more interesting.

First of all we must keep in mind that the conditions for carrying out those excitations produced by a trigger signal can change both along the entire length of the afferent-efferent pathway and also in individual links within it. It is natural to think that changes in the conditions of the performance of the excitation in motor portions of the pathway can hardly find any reflection in the behavior of the alpha rhythm of the visual occipital region of the cortex. Moreover, these changes can be expressed in a significant manner in the values of the latent periods of the reactions. On the other hand, it is highly likely that changes in the conditions of the performance of the stimulus in the optical analyzer are not only reflected in the changes of the latent periods of the visual motor reactions but can also be closely linked to the behavior of the alpha rhythm in the occipital region.

If we look from this point of view at the data which were obtained by Stamm, we can reach the following conclusions: The fact that the latent periods of depression of alpha rhythm under the conditions of this experiment are limited only to the transition from conditions "a" to conditions "b", may indicate that the conditions for the performance of the excitation in the afferent link of the nervous pathway change only with transition from conditions "a" to conditions "b" and do not undergo further changes of any kind with

a transition to conditions "c" and "d". With regard to the causes of the shortening of the latent periods of the motor reactions with transition from conditions "b" to conditions "c" and then to conditions "d", this means that they must lie in the changes in the conditions of the performance of the excitation in the subsequent links of the visual-motor pathway.

It is interesting to note still another fact. According to Stamm's data, the latent periods of depression of the alpha rhythm are uniform under conditions "b" and conditions "c", i.e., in the absence of both simple and differentiation reactions. At the same time, other authors who also worked with visual signals report a lengthening of the latent periods of blockage of the alpha rhythm with transition from the performance of a simple reaction to the performance of differentiation reactions. Such data were obtained, for example, in the investigation by Knott (1939).

An analysis of the experimental conditions of the two authors /235 mentioned shows that the differences which they noticed are not random but are regularly related to the different nature of the differentiation in the two experiments. In both cases, a flash of light served as the positive signal for the differentiation reaction. In Stamm's experiment, however, sound served as the inhibitory signal, while in Knott's experiment the flash of light was used once again but was given in the other half of the visual field. Hence, in Knott's experiment, the subject was subjected to significantly sharper differentiation than in Stamm's experiment. Therefore, we may conclude that with a transition from a differentiation of different stimuli (belonging, for example, to different analyzers) there is a change in the functional state of only the motor portion of the nervous pathway, which naturally does not entail any reflection in the performance of the alpha rhythm of the occipital region. However, with the transition to differentiation of similar stimuli addressed to the same analyzer, the functional changes take place over the very same region of the pathway, beginning with its afferent link.

An analysis of the work of Stamm gives us reason to digress somewhat and mention that insufficient attention to the concrete mechanism of the production of the reaction not only impoverishes the results of a given paper but can even lead to erroneous conclusions. Thus, in the investigation of Lansing, Schwarz and Lindsley, the results of which have already been mentioned briefly by us before, it was shown conclusively that if the warning signal causes depression of the alpha rhythm in the occipital region of the cortex, the latent period of the visual-motor reaction will be shortened significantly. On the basis of these data, the authors concluded that there is a close relationship between the depression of the alpha rhythm in response to a warning signal on the one hand, and the values of the latent periods of the corresponding reaction on the other. Nevertheless, in a very recent paper by Hermelin and Venables this conclusion was questioned, inasmuch as in their experiment they did not observe any kind of definite relationship between

the presence or absence of the blockage of the alpha rhythm after a preliminary signal and the value of the latent periods of the motor reactions (Hermelin and VENABLES, 1964).

However, if we carefully examine this paper we can notice the following fact. The authors, recording the alpha activity in the occipital region of the cortex, used auditory stimuli as triggering signals for the motor reactions. A legitimate question arises: Why and how do the neurophysiological changes taking place in the visual cortex under the influence of warning signals and finding their expression in the blockage of the alpha rhythm, have a regular influence on the speed of performance of the auditory motor reactions? In fact, the state of the visual cortex is not related in any regular manner to the rate of transmission of the stimulus from the auditory analyzer to the motor analyzer. However, insufficient attention paid to the specific mechanism of the production of the reactions and to analysis of the nervous structures by which excitation is propagated, led the authors to an inadequate method of investigation and (as a result) to an erroneous position which contradicts the data obtained and the facts observed in the work of Lansing, Schwarz and Lindsley. /236

The cause of the depression of the cortical rhythms under the influence of different kinds of stimuli at the present time is believed to be connected with the impulses which arise in nonspecific structures of the subcortex. In addition, all the facts presented above clearly show that verbal stimuli in man have a very important influence on the parameters of depression. Thus, these facts make it possible to believe that in man, among the important factors which take part in the complex reactions leading to depression of cortical rhythms, we must include verbal stimuli and the inter-central impulses produced by them. Therefore, in this case it is particularly important to dwell on those works (unfortunately, only a few) of authors who analyzed the electro-physiological data from the same point of view.

The study of O.M. Grindel and B.G. Spirin is entitled: "The Reflection in the Electroencephalogram of the Inhibitory Effect of the Secondary-Signal System on the Final Motor Effect" (1960). The authors carried out three series of experiments in which they obtained similar data. We will discuss two of these series.

(1) The subjects were given 10-20 successive auditory signals, one to two seconds apart. Each signal, except for the last one, was accompanied by the command "Push!", in response to which the subject carried out a motor reaction. Under these conditions, towards the end of the auditory signals there was definitely observed a formation of a auditory-motor time link. In the absence of the verbal warning for the last signal, this link could be seen and actually appeared frequently as a motor reaction to the signal when not accompanied by the command "Push!". However, in a number of cases the link was retarded (in the opinion of the authors) by the

secondary-signal system and the motor reaction to the nonreinforced signal was absent.

The authors note that in all the methods of recording which they carried out (occipital, parietal-occipital, parietal-frontal and central), depression of the basic rhythm was noticed in response to the last signal at a time which corresponded to the stereotyped delivery of the verbal warning. The conditioned motor reaction was absent. On the other hand, if the motion was completed, depression /237 occurred after completion of the reaction.

In the case of the depression of the basic rhythms in the absence of the conditioned motor reaction, the authors see an inhibitory effect of the secondary-signal system for the following reasons:

(a) The earlier time of the appearance of depression, which makes it possible to consider the impulses responsible for it as causing the absence of motion, and

(b) a stronger manifestation of depression in the parietal-frontal region.

(1) Auditory signals were given in groups at intervals of one second. According to the preliminary instructions, the subjects pressed a button after every third signal. From time to time, the stereotyped delivery of the stimulus was changed: the warning for the third signal was not given. Under these conditions, erroneous, i.e., premature, motor reactions sometimes occurred and sometimes did not. As in the preceding series, if when the third signal was given at intervals of one second, a depression of the basic rhythms of the cortex was noted, there were no erroneous motor reactions. However, if the signal was given and the background activity did not change in any way, the usual motor reaction occurred. This relationship was particularly clear and regular in repeated omission of the warning for the third signal, which the authors believe to be related to an increasing role of the active secondary-signal control of reactions after the first change in the stereotype.

O.M. Grindel and B.G. Spirin point out that regular depression of the alpha activity cannot be explained by an orientation reaction to the change of the stereotype, inasmuch as the phenomena mentioned did not vanish with repeated omissions, but rather were reinforced and frequently were in advance of the moment corresponding to the time when the third signal was given. The authors feel that their data give a completely reliable picture of the possibility of an indirect reflection of the activity of the secondary-signal system and the electrical activity of the cortex.

The most direct reflection in the electroencephalogram of the secondary-signal control impulses was shown in the investigation of M.P. Ivanova and F.M. Talyshev (1964). In these experiments, the subjects were required (in response to an auditory signal) to accu-

rately exert a force of 20 kilograms with their right hand. In some cases the experimenter indicated whether or not an error had been made and in others he did not. When the verbal correction was given, there was a shortening of the time of the active contraction of the muscles, along with a lengthening of the latent period of the muscular reaction and an increase in the duration of depression of the alpha and Roland rhythms. The most important and statistically significant increase in the duration of depression took place in the sensory-motor regions. Consequently, in these investigations there was a direct indication of a relationship between the intensity of the secondary-signal effect with respect to the motions performed and the duration of the depression of the Roland rhythm. /238

Significant increase of the period of depression of the alpha rhythm in response to light signals under the influence of special verbal instructions was also pointed out by N.A. Mushkina (1965). According to her data, instructions to follow the appearance and development of a visual after-image can sometimes increase the duration of the depression of the alpha rhythm in response to a light flash. The phenomenon is apparently analogous to the prolonged depression of the alpha rhythm when the subject is required to observe objects in a dimly lit room (Jasper and Cruikshank, 1937) and it must be related to a prolonged impulse of secondary-signal nature with respect to the visual cortex, which increased its excitability.

In the light of the data and concepts discussed above, special attention should now be paid to the investigations of M.P. Ivanova in connection with the values of the latent periods of the motor reactions in response to light stimuli, on the one hand, and the duration of depression of alpha rhythms in response to these stimuli on the other. M.P. Ivanova found that even with the most diverse changes in the conditions of the experiment, there is always an identical change in the values of the latent periods of the motor reaction in response to light signals and the duration of depression of the alpha rhythms in the occipital region. (Ivanova, 1962a, 1962b). The regularity consists in that the shortening of the latent periods of the motor reactions is always accompanied by a shortening of the period of blockage of the alpha rhythm, while lengthening of the latent periods of the motor reaction is always related to a lengthening of the period of depression.

It is clear that these data can be compared with the theories which we have developed regarding the mechanisms of the production of motor reactions under the conditions of a limited number of signals. As has been pointed out repeatedly, the leading role in the production of such reactions was formerly assumed to be that of the prepared changes in the excitability of the nervous pathways along which the stimulus travels from the receptor to the effector. The theory which has been developed suggests that we can naturally assume that the greater the reaction which is prepared, the more rapidly it is carried out. However, at the same time we must point out that there must be a corresponding reduction in the role of

the secondary-signal impulses which regulate the process as the reaction is being performed. If we assume, on the basis of the papers mentioned above (Ivanova and Talyshchev, Mushkina et al.), that the duration of the depression of the alpha rhythm constitutes a reflection of the duration and intensity of the secondary-signal effects arriving at the analyzer, then clearly the facts described by M.P. Ivanova can serve as a confirmation of the theory which has been developed, though indirectly. /239

The effect of the secondary-signal impulses on the direct visual projections has also been specially studied in the investigation of E.A. Golubeva (1961), who showed that preliminary verbal instruction can have a significant effect in changing the electrical effect of adoption of rhythms. In E.A. Golubeva's interesting experiments, the subject was presented with pairs of visual complexes. The light stimuli involved in the complexes had a rhythmic character. The frequency of stimulation corresponded to the optimum frequency of the establishment of a rhythm for each subject, and was specially determined in preliminary experiments. In the experiments, two complexes appeared successively, which either had a common element (a lamp which was switched on in both the first and second complexes) or did not. The effect of the establishment of rhythms was determined under conditions when the complexes were presented without instructions of any kind and under conditions when instructions were given which required the subjects to pick out the common component in the complexes.

The experiments showed that when instructions were given the effect of establishment of rhythm increased significantly and was at its maximum during presentation of a second complex which shared a common component with the first. Inasmuch as the rhythms mentioned are actually a variation of the evoked potentials (Kozhevnikov and Meshchenskiy, 1963) the data of E.A. Golubeva can be ranked along with the facts considered above pertaining to the influence of verbal instructions on the primary and secondary responses.

§3. Secondary-Signal Control Impulses and Sensitivity of Analyzers.

Numerous papers in recent years indicate that the sensitivity of the analyzer systems is much more complex a function than was thought earlier.

In the first place, there is a definite difference in the excitability of various links in the ascending afferent pathway. Hence, the higher the level of the analyzer through which a given reaction selected by the experimenter takes place, the higher will be the characteristics of the sensitivity, since it reflects the state not only of the given level of the analyzer but of all those located below it. It is all the more important to take this condition into consideration in view of the fact that in a number of cases, under the influence of various conditions, changes in the

excitability of structures located above and below the analyzer can have contrary and differently directed natures. Thus, light, which lowers the sensitivity of the receptors of the retina, increases the excitability of the cortical cells of the visual analyzer; darkness, which increases the sensitivity of the peripheral apparatus, lowers /240 the sensitivity of the central analyzer structure.

In the second place (and this is most important), there are many regulatory mechanisms which change the functional conditions of the structure of the analyzer within broad limits. Some time ago it was believed that the reception of stimuli (including very weak ones) is not limited by the transmission of impulses along a direct afferent pathway but is determined by the overall condition; the activity of the organism relative to the stimulus depends on its behavior at any given moment, and so on. However, for many years the idea of the activity of the organism with respect to the active stimuli has been limited to basic recognition of the importance of the local action of adequate stimuli (adaptation) and some externally manifested adaptations and adaptative reflexes (for example, the narrowing of the pupil under the influence of light and the direction of the eyes or ears toward the direction of the stimuli). However, it was suggested relatively long ago that there are other, deeper mechanisms which regulate the activity of the analyzer system. An important reinforcement for such a point of view was the data presented at the very beginning of the century by morphologists, dealing with the existence of centrifugal fibers running downwards in the substance of almost all afferent pathways (at the present time, it is known that in fact all the pathways are involved).

However, physiological investigation of the mechanisms of the central regulation of activity of analyzers has begun relatively recently. It follows several trends; the investigations have significantly enriched our previous ideas regarding the regulation of the activity of analyzers. Among the principal directions along which investigation of this problem is proceeding at the present time, we can mention the following:

(1) Investigation of the diverse reflectory changes in sensitivity under the influence of stimuli to different organs of sensitivity (Kravkov, 1948, 1950), investigation of the reflex interactions between the various systems of the very same analyzer (Orbeli, 1934; Lebedinskiy, 1938, et al.), investigation of reflectory changes in sensitivity of a structural nature (Snyakin, 1961; Zayko, 1956; Belikova, 1957, Kurilova, 1950; Yesakov, 1961) and (to a certain extent) the changes in the dimensions of the respective fields of the retina (Glazer and Zuckerman, 1961). The structural changes in the sensitivity are included in the activation and mobilization of a large or small number of receptor elements or in changes in the cortical characteristics of the neuron, in which convergence of impulses from the receptors occurs. The changes which take place are such that the functional level of the receptor apparatus is found to have maximum correspondence to the demands of the internal milieu

and the internal condition of the organism.

(2) Discovery and investigation of the sensory conditioned reflexes, i.e., those conditioned reflexes which affect the functional condition and frequently the sensitivity of the analyzer systems as well (Dolin, 1936; Bogoslovskiy, 1936; Kravkov, 1950 et al.). /241

(3) A dissemination of the ideas of L.A. Orbeli about the adaptation-focus function of the vegetative nervous system on the activity of the sense organs and all parts of the central nervous system (Orbeli, 1938; Rappaport and Robinson, 1936; Arkhangel'skiy, Gol'ts and Rayeva, 1936; Zagorul'ko, 1927; Tonkikh, 1930; Asratyan, 1930). Among the later works which tend in this direction we should mention the investigations of Loewenstein (1956) and Chernetskiy (1964). Loewenstein found that stimulation of the sympathetic nerve innervating an isolated piece of frog skin increases the sensitivity of the tactile endings. This is manifested in a reduction of the threshold of the appearance of afferent discharges, and an increase in number and the duration when stimuli above the threshold level are used. Chernetskiy observed the same effect when he stimulated the sympathetic fibers in an intact preparation. It was also shown that stimuli of other types can have the same kind of an alleviatory effect with respect to the skin reception of the frog. These include painful stimuli. Chernetskiy determined the following important fact: The reflex action of these very different stimuli is effected by sympathetic fibers, since it vanishes in pieces of skin which are deprived of sympathetic innervation.

(4) The discovery and investigation of direct central influences with respect to ascending afferent impulses. This line of investigation has been developed intensely since Leksell in Granit's laboratory showed that the selected stimulus of thin efferent fibers (gamma efferents) in the substance of the anterior roots of the brain does not produce contraction of muscle but causes afferent discharges in the posterior roots (Granit, 1957). Further investigation of this point has shown that the gamma efferents (within wide limits) regulate the frequency of the discharges arising in the proprioceptors (muscle spindles) when the muscle contracts, and that corresponding effects such as alleviating and inhibiting effects can be produced by electrical stimulation of various central structures. Moreover, the existence of central control was shown for all sensory systems and for all the levels of the input pathways connecting the receptors and switching nuclei (see the works by Livingston, 1959, 1962; Narikashvili, 1962, 1963; Pilipenko, 1961). As far as the cortical cells of the analyzers are concerned, their excitability may in turn be controlled by other portions of the brain, partly by the reticular formation and thalamic nonspecific system (Li, 1956); Young, 1962; Bremer and Stoupel, 1959; Narikashvili, 1962, et al.). /242

At the present time, the work which is proceeding in this direction is still quite limited. A combination of these investiga-

tions and a clarification of the concrete role of the changes in the functional state of the analyzers and the concrete significance of a given regulating mechanism in purposeful action, constitutes a problem for the immediate future. In solving this general problem as it applies to the behavior of man, a significant place must be given to the investigation of the study of the regulatory function of the secondary-signal system in the operations of the analyzers. "One of the features of the dualism of the old physiology of the sense organs" wrote A.M. Maruseva and L.A. Chistovich in this regard, "was the principal delimitation of the direct measured stimuli used in the experiment (sound, light, etc.) and the verbal signals from the experimenter. If the former of these were considered as physiological events and their influence was studied carefully, the second were not assigned at all to the field of physiology and were considered as merely psychic effects. Their influence on the results of the experiment was not studied" (Maruseva and Chistovich, 1964, p. 465).

All of the experimental data which constitute the subject of the analyses of the present monograph naturally can and must be viewed also in the context of a system of diverse mechanisms, regulating the activity of the analyzer. In this chapter we propose to deal particularly with those investigations in which it was shown that changes in the functional state of the analyzer which arise under the influence of the verbal stimuli are clearly evidenced by changes in sensitivity, i.e., changes in the threshold characteristics of the stimuli which evoke these reactions. The analyses of these investigations show clearly that the secondary-signal control impulses play an important role in the process of detection of weak signals.

Many investigators, concerned with the study of the problems of sensitivity in man, have turned increasing attention to the fact that the secondary-signal stimuli play a very important role in the quantitative indicator which measures the value of the absolute and differential thresholds. For example, V.G. Samsonova, on the basis of her experiments in the study of sensitivity in man, reaches the following conclusions: "In adult man, the secondary-signal system contributes to a detailed analysis of the primary signal system, which makes it possible to analyze and synthesize the former and ultimately makes it possible to carry out more adequate reactions to external stimuli (Samsonova, 1958, p. 138)".

We will begin an analysis of the materials available here with /243 one of the most important investigations by A.M. Maruseva (1955). In this study, which included several experiments, the investigators recorded the threshold of the appearance of a verbal reaction to weak sound stimuli as well as the threshold for the appearance of a cutaneous galvanic reflex and reactions of eye movements toward the source of the sound. In the case of the first sound signals used, it was observed that the verbal reactions of the subject, by which he reports the presence of the sound, occur at higher intensities

of the stimuli than do the cutaneous galvanic reflex and the eye movement reaction. This difference, which on the average amounted to 10 db, gradually decreased and finally fell to zero. In various subjects, this required from one to three experiments (from 30-45 to 90-145 presentations).

However, if a preliminary instruction (which the subjects received along with the request to report on the presence of the sound) also contained a very concrete and detailed indication of the nature of the sound signals used (the subjects were required to report the presence of extremely weak intermittent sound signals delivered to the right ear), there was no difference in the threshold of the appearance of various reactions. In these cases, the threshold of the verbal response to the first sounds given practically coincided with the threshold of the cutaneous galvanic reflex and the eye movement reaction in the direction of the source of the sound. It is also interesting that under these conditions we did not observe any kind of an increase in sensitivity as a function of the repetition of the experiments for any one of the reactions used.

On the basis of these data, we may conclude that an increase in sensitivity recorded with verbal or performance motor reaction during prolonged application of weak stimuli (sensitization, according to Bronshteyn, 1946) connected with the verbal qualifications of the characteristics of the signals used. Only under the usual conditions was such a qualification developed gradually by a given subject as a function of repeated presentations of weak signals, while in A.M. Maruseva's experiments the tests were extended to a measurement of sensitivity.

The significance of this verbal qualification of the characteristics of the weak signals used (in our opinion) consists in the fact that corresponding positive control secondary-signal impulses are set in motion which increase the sensitivity of certain afferent structures and likewise increase the probability of the appearance of weak signals. We propose that in the given case we must be dealing mainly with positive secondary-signal impulses of a tonic nature which constitute the previously prepared warning increase in sensitivity of certain afferent pathways, related to the signals employed. There may be a very local and selective increase in the sensitivity of the analyzer which corresponds closely to the projection of the weak signals applied in the experiment. Thus, A.I. Bronshteyn showed that with prolonged presentation of a tone of a given volume directed to one ear, sensitization was observed with respect to this tone and this ear alone, since no reduction in sensitivity was observed when other tones were used, directed to the other ear. The same effect was described by A.I. Bronshteyn with respect to visual signals, distributed in different parts of the field of vision. Prolonged use of one and the same specific visual stimulus (for example, located at a point corresponding to 18° of the periphery) caused a drop in the threshold with respect to this stimulus, at the same time that presentation of other signals (for example, located

at 5° and 10° of the periphery) did not cause any increase in sensitivity.

From what has been stated above, it is clear that all the factors which reinforce the positive secondary-signal impulses and permit an increase in their effect in direct projection must necessarily lead to an increase in the sensitivity of the analyzer. Among such factors we can include special instructions which stimulate the subjects as far as observing the extremely weak signals is concerned.

In the investigations of E.N. Semenovska (1947), the instruction "Please look with all your attention" in conjunction with the preliminary signal "Attention!" caused an increase in the threshold sensitivity of about 25%. In the same category we must include (at least partially) those instructions in which it is found that the subjects received a higher payment after the experiment when they achieved lower thresholds (Blackwell, 1952). Preliminary signals of another type, which adapt the activation of the secondary-signal control impulses at the moment of administration of weak stimuli, also lead to a considerable increase in sensitivity (Maruseva and Chistovich, 1964; Maruseva, 1959; Chistovich, 1956 et al.). The shorter the interval between the preliminary signal and the stimulus being tested, the higher the sensitivity (data of Neville, quoted by Woodsworth, 1950, p. 316; Howarth and Treisman, 1958).

We must conclude that the value of the preliminary signals is not limited by the fact that they lead to complete immobility of the subject and at the same time cut out background noises (Maruseva, 1959). If the matter were limited to only these factors, the preliminary signal would also have to increase sensitivity to all possible signals, both sound and visual. However, the local shift in sensitivity mentioned above observed in the works of A.I. Bronshteyn, for example, contradict this conclusion. Therefore, the principal value of the preliminary signal must be seen in the activation of the secondary-signal impulses (more local or more generalized, depending on the nature of the direct stimuli applied). /245

The definite difference between the effects of the secondary-signal control impulses in our experiment in measuring the local excitability and in experiments in investigating sensitivity is also manifested in the following fact: As has been shown, the effects of the positive secondary-signal control impulses weaken when the number of points of their application are increased as a function of the negative-induction relationship between the path of the propagation of the excitation and the corresponding points of the analyzer. This position is valid for both the special secondary-signal impulses which occur and for prolonged actions (for example in carrying out motor reactions in response to preliminary instructions). One of the observations of A.I. Bronshteyn is very relative in this respect. In one of his experiments he noted (and later experimentally proved) that sensitization to weak sounds does not occur if

several tones of different volume are used during the experiment, rather than one tone of a given type, as is usually done. It was necessary to conclude that there we have the same phenomenon as in the experiments with the motor reaction; however, the local preliminary differences in sensitivity of a positive character are reduced and can even vanish with an increase in the number of possible signals.

In this respect, we may recall the data obtained by Blackwell (1952). In his experiments, he measured the contrasting sensitivity of the eye. Changes in brightness of a bright spot could take place either at one point in the visual field (at a distance of 7° from a fixed point) or at four points (located at the same distance). The results of the experiment showed that with high motivation (the subjects received an increased reward if they attained minimum threshold values) the contrast sensitivity was much higher in 6 out of 8 subjects when the weak signal was given only at one point in the visual field. Contradictory data obtained in the other two subjects most likely were caused by the influence of some other supplementary factors, inasmuch as all of the thresholds were much lower in one of them and much higher in the other than in the remaining subjects.

This fact, that the value of the location of a weak signal which must be observed is strongly dependent on the success of the observation, has been thoroughly investigated by practical workers using signal lights. In his book, "The Basis of Visual Intermittent Signaling" R.L. Fob'l writes on this topic: "The observation of light under field conditions may differ sharply from observation as determined under laboratory conditions. Under laboratory conditions, the place at which the light will appear is nearly always known, and consequently the probability of observing it after a given time is greater than under practical conditions, when the location of the light is unknown" (Fol'b, 1964, p.59). According to the data presented in R.L. Fol'b's book, an increase in the threshold with a transition from the condition in which the place where the light will appear is known to the condition in which it is unknown, on the basis of the reports of various authors, runs from 21-200 to 300%. Even if we discard the uncertainty which always exists under practical conditions, regarding the direction of the observers gaze and his search for a weak signal by moving his eyes and head, nevertheless we must conclude on the basis of all the facts which have been set forth that an important place in the increase in sensitivity to the signal whose location is well known in this case also must be assigned to the very significant effect of the positive secondary-signal impulses. /246

The materials and conclusions set forth above easily lead us to the conclusion drawn by A.M. Muruseva on the basis of a number of experimental data (Muruseva, 1965). This conclusion consists of the following: Usual experiments in measuring sensitivity in man must be viewed as one of the situations in which there is an occurrence of reactions to preliminary instructions. As a sign of the reactions corresponding to the instructions, in this case we have either a weak stimulus or a very weak difference between the stimuli, and the response is a given speech act or motion.

Inasmuch as the voluntary reactions of man always take place by means of control secondary-signal impulses which are directed to certain points or areas of immediate projection, according to requirements of the instructor, the nature of these requirements may have a definite effect on the results of measurements of sensitivity. The degree of such an effect was the subject of a special investigation in the work of Fernberger, who studied the different thresholds of differentiation of weight (Fernberger, 1931). In his experiments, Fernberger used a standard 100-gram weight placed in one hand of the subject, while in the other hand he placed various objects whose weights could be less than, more than, or equal to the standard. Using an absolutely uniform procedure of carrying out the experiment as far as the presentation of the comparison stimuli was concerned, the subjects in different groups received different preliminary instructions of three kinds.

(1) Neutral or standard instructions, according to which the subjects replied "Heavier", the second weight was heavier than the first), "Lighter" (*vice versa*) and "Same" (in case the two weights were equal).

(2) Instruction which was specially intended to reduce the number of equal estimates. The subjects, in addition to the responses "Heavier" and "Lighter", had to say "I don't know" if the results of the comparison could not be assigned to either of the first two groups.

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(3) Instruction especially intended to increase the number of equal estimates. The subjects classified the differences into three categories as in the standard instructions **but** they were warned in advance that they should say "Heavier" and "Lighter" only when they were absolutely sure that this was really the case.

We should mention that the result, relative to the possibility of making a fine distinction in weight, turned out to be quite different in subjects in these three groups. It amounted to 2.12 grams for the subjects who received the second instruction, 4.34 grams for those who worked under conditions of the first instruction, and 9.80 grams for the subjects who received the third instruction.

On the basis of the results he obtained, the author drew the completely correct conclusion that in all psychophysical work extreme attention must be paid to the formulation of the instruction and to the possibility of determinance in the interpretation by the subject of usual standard instructions. Moreover, in the opinion of Fernberger, the subject is often observed to be undetermined to a significant degree and to make different interpretations which can easily cause significant differences in the results obtained. As far as the concrete physiological mechanisms are concerned, which cause the differences observed in Fernberger's experiments, we believe that they must be viewed in a different nature and under different conditions of performance of the differentiation reaction by

the subjects in response to preliminary instructions.

In all of these cases, in Fernberger's experiments, the subjects were required to differentiate three groups of stimuli. One group was the correlation of stimuli when the weight used was heavier than the standard. The second was formed when the weight was lighter, and the third group consisted of those stimuli which made up some category between the first two. However, this intermediate category was already determined earlier in the instructions, either as being extremely narrow (including only those signals which could not be differentiated from one of the other two, or very wide (including even those signals which could be related to one of the other two groups but whose assignment was not completely certain).

We can interpret similarly the data obtained in one of the experiments in determining the differentiation threshold for sound signals against a noise background (House and Melrose, 1956). In these experiments, against a background of a constant noise, a weak sound signal might appear at a certain moment. The subject was warned in advance about the time when the sound signal might appear, by means of a special stimulus. In 50% of the cases the sound actually did occur, but in 50% it did not. Two groups of subjects participated in the test. The subjects in the first group were told to press on a key in all situations when they noticed the presence of a sound. The subjects in the second group, on the other hand, were supposed to press the key only in those cases when the sound was absent (in their opinion). /248

It was found that the threshold of observation of the sound signal for the subjects in the second group was about 2 db lower than in the subjects of the first group. This fact can be understood if we assume, as is done in psychophysiology, that between the time when the stimulus is actually present (at a sufficient intensity) and when it is actually absent (at a very low intensity) there is a short interval of uncertainty. However, if (in the experiments under consideration) the subjects did not press the key in uncertain, doubtful cases, then for the subjects in the first group only those sounds served as signals for a reaction whose intensity exceeded the doubtful cases, and for the subjects in the second group only those sounds served as signals which were weaker than the doubtful ones. Hence, it becomes understandable why the threshold force of the stimulus which leads to the performance of a reaction was found to be less in the subjects of the second group.

A similar interpretation of similar experimental facts is contained in the investigations of K.V. Bardin, who used a method of measuring differential thresholds (Bardin, 1960). K.V. Bardin paid special attention to the considerable differences in value of the differential thresholds obtained by using a method of minimum changes, depending on whether the subjects were asked to name the moment when the difference appeared or the moment when the difference disappeared. In the second case, the difference noted regularly turned

out to be less than in the first case. According to K.V. Bardin, this takes place because the reactions in these two cases are on different sides of the interval of uncertainty. As in the preceding investigation, the signal (according to the instructions) in some cases was only the definite difference, while in others it was only the definite absence of a difference. Of course, it is completely natural that the value recorded by the experimenter for the differences noted by the subject turned out to be greater in the first case and less in the second.

Apparently we can similarly understand the data which were obtained for the absolute sensitivity when using different instructions. We have in mind the investigation by Smith and Wilson (cited in Rosenbluth, 1961), in which three different types of instructions were used in measuring the absolute auditory sensitivity: "radical", "liberal" and "conservative". The conservative instruction told the subjects to notice the appearance of a sound only in a case when they were completely sure it existed; the radical instruction meant that the subjects must give a signal in all cases when they felt that there was the least possible possibility of its presence; the liberal instructions had a intermittent character. /249

The results of the measurement showed that the difference in the threshold in the extreme types of instruction reached 10 db, reaching 8 db for the radical and liberal instructions and 2 db for the liberal and conservative. We must conclude that here, as in the experiment considered above, with different sensitivity the definite stimuli were sometimes included and sometimes not included among the signals, according to the demands of the preliminary instructions. Therefore, we believe we must agree with the point of view of L.A. Chistovich, who states that in experiments studying absolute sensitivity, the subjects not only were required to observe the weak signal but also to differentiate it from other additional or background stimuli (Chistovich, 1956). As far as the nature of the positive stimulus under conditions of differentiation is concerned, we see from the facts set forth above that it can be established in different ways by preliminary verbal instructions.

In the light of the data set forth, above, we should pay very serious attention to the statistical mathematical theory of observation of weak signals set forth by Svets, Tanner and Birdsall, 1964. The principal feature of this theory (which is of the greatest interest, as the authors themselves point out) is that it makes it possible to make a quantitative determination of the criteria used by the observer when he assigns certain events to the signal category and others to the noise category.

The authors are completely correct when they point out that until now, in all experiments in measuring sensitivity, there were two independent and different factors which were mixed and not separated. One of them was this actual sensitivity which can be understood (conditionally, it must be admitted) as the ability of a sen-

sory system to make responses of a definite force or amplitude to the action of weak stimuli. The second factor is the criterion on the basis of which each response given by the sensory system is assigned by the observer either to the signal category or the noise category. The mathematical model formed by Svets, Tanner and Birdsall makes it possible to characterize differentially these different aspects of the observation of weak signals by the observer. At the same time, an analysis of the concept of the idea of "criterion" in the theory proposed shows that the criterion actually turns out to be no more than the characteristic of the width of the zone of the signals in the direction of the weak responses of the sensory system. The narrower this zone is, the higher and stricter the criteria and the fewer spontaneous responses of the sensory system which will reach the zone of the signals. The wider the corresponding zone, the lower the criteria and the more frequently the noises will be understood as signals. /250

Hence, there is a justified parallel between the results of certain experiments which were discussed above and the results of a statistical theory of making decisions about weak signals observed. In the works by Fernberger, Smith and Wilson discussed by us above, the width of the zone of the signals for certain sensory excitations, i.e., the value of the criteria, from the very beginning was set more or less exactly by the verbal instructions of the experimenter. Under other conditions, to a certain extent in the experiments conducted by Svets, Tanner and Birdsall, the criteria for definite self-instruction were worked out by the subjects themselves in the course of the experiment. The value of the criterion is influenced by factors such as the probability of the appearance of the signal, the value of the reward for the signals observed and the value of the punishment for signals missed and for erroneous reactions. Hence, the criteria here are the results of many factors, including the relationship of the observer to the experiment and several features of his personality (however, these factors are equally involved in experiments using the criteria given earlier). This resulting value of many factors is usually very close to the optimum value of the criterion in any given combination of experimental conditions, as established by theory for the ideal observer.

We believe that if the behavior of a real observer can be described sufficiently well by a mathematical model of an ideal observer, then perhaps the behavior of a real observer, optimally prepared for the conditions of the preliminary signal, can be controlled without the interference of his verbal thought. On the other hand, we think that the corresponding self-instructions are certainly developed with the active participation of secondary-signal mechanisms of reflection, located at the basis of the verbal thinking of man. But after the criterion is worked out, perhaps there will be some kind of a difference in the mechanism of its influence on the progress of the experiment under these conditions by comparison with the conditions with the criteria given earlier. We believe that this mechanism, as in other cases of reactions in man,

must include certain combined effects of tonic and phasal secondary-signal control impulses. It can be described in most general terms as follows: On the one hand, a difference in the excitability of the signal and noise zones can be formed by means of secondary-signal control impulses of a tonic nature. On the other hand, at every moment when the observer can be given a weak signal, phase secondary-signal positive impulses must be directed into the analyzer which /251 locally increases the sensitivity of the direct projections according to the verbal qualifications of the desired signal. They also increase the frequency of the discharges produced in the neurons of the sensory system by a weak stimulus. We may believe that "the margin of success" or "margin of error" of these reinforcing impulses can be different, and it is precisely these differences which, in our opinion correspond to the different values of the criteria in the system of logical-mathematical understanding. This "search margin" in the cases of absolute sensitivity of the vision and hearing, apparently can be related to the force of the positive control impulses as far as the projection of weak signals is concerned.

The proposed physiological interpretation of the mathematical theory of Svets, Tanner and Birdsall apparently makes it possible to overcome one essential difficulty which thus far has arisen in applying the theory to human activity. We are talking about the fact that in this interpretation, which the authors give to responses of the sensory system and the criteria, unquestioned phenomena of psychic activity in man disappear (such as the perception and transition from the feeling of perception to actual perception). However, a comparison of theory with ideas of the actual and complex nervous mechanisms lying at the basis of the detection of weak signals shows that actually this theory is no less plausible than any other. In any case, within the scope of this theory it is completely possible to show the location of the sensations, "these most simple subjective signals of an objective relationship of the organism to the external world" (Pavlov, 1951, vol. 4, p. 123).

By the same token, excitability is the instrument which, in higher nervous activity of man, during reception of weak stimuli, assigns some sensory stimuli to the signal category and others to the noise category. We can then suggest the following: As a function of the decrease of the excitability of the system, the sensory neurons simply cease to be discharged by impulses, both in response to specific afferent stimuli, the value of which do not increase a certain limit, and as a response to a different kind of supplementary intracentral impulses. The probability of the appearance of a discharge finally depends on the force of the impulses which arrive. If the cortical neurons emit impulses of a certain value, this produces a sensation which is the suggestive signal of a weak stimulus. When the excitability of the sensory neurons is increased, they emit impulses in response to increasingly weaker stimuli, regardless of their source. Consequently, the sensation arises here with continually decreasing force of the afferentations arriving at the neurons. Hence, we may conclude that with decreased excitability

of the analyzer systems the person actually "does not see" the weak stimuli, while with increased excitability he "sees" signals which are not there. In the hypothesis which we have set forth, we likewise relate the sensitivity of the sensory system to the threshold of the appearance of local post-synaptic potentials in the neurons, but the criterion is from the threshold of the appearance of the propagating discharge of the impulses (Chapter 1). Since it is clear that from the moment when the local post-synaptic potentials appear until the moment when the propagating discharges appear in the neuron, a certain period of time passes, the suggestion which has been made obviously can be related generally to a model proposed by M.B. Mikhalevska (1964). According to this model the channel of transmission of sensory information has two successive thresholds, the second of which coincides with the criterion of the observer. /252

We believe that all the data given above do not contradict the available facts. At the same time, it makes it possible to conduct a more detailed investigation in the field of the physiology of the sense organs, contemporary methods of mathematical analyses, and general problems of the physiology of higher nervous activity in man.

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